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Cell contamination and branching process in random environment with immigration

Vincent Bansaye *

August 5, 2009

Abstract

We consider a branching model for a population of dividing cells infected by parasites. Each cell receives parasites by inheritance from its mother cell and independent contamination from outside the cell population. Parasites multiply randomly inside the cell and are shared randomly between the two daughter cells when the cell divides. The law of the number of parasites which contaminate a given cell depends only on whether the cell is already infected or not. We determine first the asymptotic behavior of branching processes in random environment with state dependent immigration, which gives the convergence in distribution of the number of parasites in a cell line. We then derive a law of large numbers for the asymptotic proportions of cells with a given number of parasites. The main tools are branching processes in random environment and laws of large numbers for Markov tree.

Key words. Branching processes in random environment with immigration (IBPRE). Markov chain indexed by a tree. Empirical measures. Renewal theorem.

A.M.S. Classification. 60J80, 60J85, 60K37, 92C37, 92D25, 92D30.

1 Introduction

We consider the following model for cell division with parasite infection and state dependent contamination. The cell population starts from one single cell and divides in discrete time. At each generation,

- (i) the parasites multiply randomly inside the cells,
- (ii) each cell is contaminated by a random number of parasites which come from outside the cell population,
- (iii) each cell divides into two daughter cells and the parasites are shared randomly into

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the two daughter cells.

It is convenient to distinguish a first daughter cell called 0 and a second one called 1. We denote by $\mathbb{T} = \cup_{n \in \mathbb{N}} \{0, 1\}^n$ the binary genealogical tree of the cell population, by \mathbb{G}_n the set of cells in generation n and by $Z_{\mathbf{i}}$ the number of parasites of cell $\mathbf{i} \in \mathbb{T}$. We write then $\mathbf{i}0$ and $\mathbf{i}1$ the two daughter cells of the cell $\mathbf{i} \in \mathbb{T}$.

First, we describe by a branching process the random multiplication and sharing of parasites in the cell, i.e. this branching process combines (i) and (iii). Second, we describe the random contamination (ii) by immigration. Finally, we combine both in an i.i.d. manner to fully describe the model.

I Parasite infection and cell division For every cell, we choose randomly a mechanism for multiplication of the parasites inside and sharing of their offspring when the cell divides. This mechanism is independent and identically distributed for every cell. Its distribution is specified by a random couple probability generating function (p.g.f) \mathbf{f} . This means that \mathbf{f} is a.s. the p.g.f of a pair of random variables taking values in \mathbb{N} .

More precisely let $(f_{\mathbf{i}})_{\mathbf{i} \in \mathbb{T}}$ be a sequence of i.i.d. couple p.g.f distributed as \mathbf{f} . For each cell \mathbf{i} , $f_{\mathbf{i}}$ gives the reproduction law and sharing of the offspring of its parasites in the following way. For every $\mathbf{i} \in \mathbb{T}$, let $(X_k^{(0)}(\mathbf{i}), X_k^{(1)}(\mathbf{i}))_{k \in \mathbb{N}}$ be a sequence of r.v. such that conditionally on $\mathbf{f}_{\mathbf{i}} = \mathbf{g}$, $(X_k^{(0)}(\mathbf{i}), X_k^{(1)}(\mathbf{i}))_{k \in \mathbb{N}}$ are i.i.d. with common couple p.g.f \mathbf{g} :

$$\forall \mathbf{i} \in \mathbb{T}, \forall k \in \mathbb{N}, \forall s, t \in [0, 1], \quad \mathbb{E}(s^{X_k^{(0)}(\mathbf{i})} t^{X_k^{(1)}(\mathbf{i})} \mid \mathbf{f}_{\mathbf{i}} = \mathbf{g}) = \mathbf{g}(s, t).$$

Then, in each generation, each parasite k of the cell \mathbf{i} gives birth to $X_k^{(0)}(\mathbf{i}) + X_k^{(1)}(\mathbf{i})$ children, $X_k^{(0)}(\mathbf{i})$ of which go into the first daughter cell and $X_k^{(1)}(\mathbf{i})$ of which go into the second one, when the cell divides. This is a more general model for parasite infection and cell division than the model studied in [8], where there was no random environment (\mathbf{f} was deterministic) and the total number of parasites was a Galton Watson process. See [15] for the original model in continuous time.

Our model includes also the two following natural models, with random binomial repartition of parasites. Let Z be a random variable in \mathbb{N} and $(P_{\mathbf{i}})_{\mathbf{i} \in \mathbb{T}}$ be i.i.d. random variable in $[0, 1]$. In each generation, every parasite multiplies independently with the same reproduction law Z . Thus parasites follow a Galton Watson process. Moreover $P_{\mathbf{i}}$ gives the mean fraction of parasites of the cell \mathbf{i} which goes into the first daughter cell when the cell divides. More precisely, conditionally on $P_{\mathbf{i}} = p$, every parasite of the mother cell \mathbf{i} chooses independently the first daughter cell with probability p (and the second one with probability $1 - p$).

It contains also the following model. Every parasite gives birth independently to a random cluster of parasites of size Z and conditionally on $P_{\mathbf{i}} = p$, every cluster of parasite goes independently into the first cell with probability p (and into the second one with probability $1 - p$).

We want to take into account asymmetric repartition of parasites and do not make any assumption about \mathbf{f} . Indeed unequal sharing have been observed when the cell divides, see e.g. experiments of M. de Paepe, G. Paul and F. Taddei at TaMaRa's

Laboratory (Hpital Necker, Paris) who have infected the bacteria *E. Coli* with a lysogen bacteriophage M13 [20]. In Section 6.1, we consider this model where a cell receive parasites only by inheritance from its mother cell. We determine when the number of infected cells becomes negligible compared to the number of cells when the generation tends to infinity.

II State dependent contamination In each generation, each cell may be contaminated by a random number of parasites which also multiply randomly and are shared randomly between the two daughter cells. This contamination depends only on whether the cell already contains parasites or not.

More formally, if a cell \mathbf{i} contains x parasites, the contamination brings $Y_x^{(0)}$ parasites to the first daughter cell of \mathbf{i} and $Y_x^{(1)}$ to the second one, where

$$\forall x \geq 1, \quad Y_1 \stackrel{d}{=} Y_x^{(0)} \stackrel{d}{=} Y_x^{(1)}, \quad Y_0 \stackrel{d}{=} Y_0^{(0)} \stackrel{d}{=} Y_0^{(1)}.$$

Moreover we assume that contamination satisfies

$$0 < \mathbb{P}(Y_0 = 0) < 1, \quad 0 < \mathbb{P}(Y_1 = 0), \quad (1)$$

which means that each non-infected cell may be contaminated with a positive probability but the cells are not contaminated with probability one.

This model contains the case when the contamination is independent of the number of parasites in the cell (Y_0 and Y_1 are identically distributed). It also takes into account the case when only non infected cells can be contaminated ($Y_1 = 0$ a.s.) and the case when infected cells are 'weaker' and parasites contaminate them easier ($Y_1 \geq Y_0$ a.s.). For biological and technical reasons, we do not make Y_x depend on $x \geq 1$. But the results given here could be generalized to the case when the contamination depends on the number of parasites x inside the cells soon as x is less than some fixed constant.

III Cell division with parasite infection and contamination We describe now the whole model. We start with a single cell with k parasites and denote by \mathbb{P}_k the associated probability. Unless otherwise specified, we assume $k = 0$.

For every cell $\mathbf{i} \in \mathbb{T}$, conditionally on $Z_{\mathbf{i}} = x$ and $\mathbf{f}_{\mathbf{i}} = \mathbf{g}$, the numbers of parasites $(Z_{\mathbf{i}0}, Z_{\mathbf{i}1})$ of its two daughter cells is distributed as

$$\sum_{k=1}^x (X_k^{(0)}(\mathbf{i}), X_k^{(1)}(\mathbf{i})) + (Y_x^{(0)}(\mathbf{i}), Y_x^{(1)}(\mathbf{i})),$$

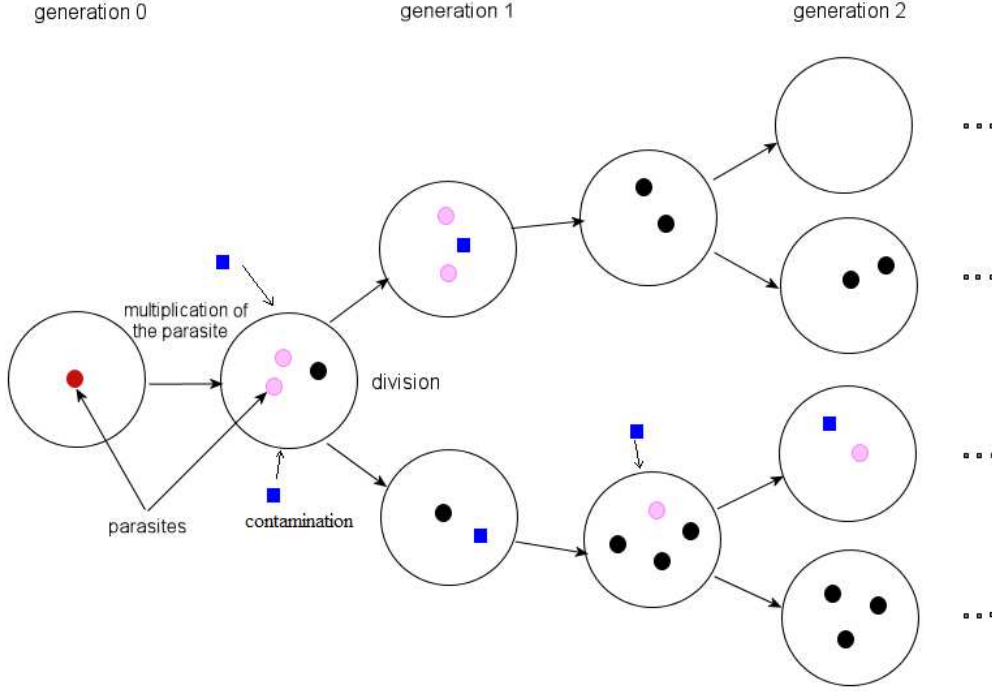
where

(i) $(X_k^{(0)}(\mathbf{i}), X_k^{(1)}(\mathbf{i}))_{k \geq 1}$ is an i.i.d. sequence with common couple p.g.f \mathbf{g} .

(ii) $(Y_x^{(0)}(\mathbf{i}), Y_x^{(1)}(\mathbf{i}))$ is independent of $(X_k^{(0)}(\mathbf{i}), X_k^{(1)}(\mathbf{i}))_{k \geq 1}$.

Moreover, $((X_k^{(0)}(\mathbf{i}), X_k^{(1)}(\mathbf{i}))_{k \geq 1}, (Y_x^{(0)}(\mathbf{i}), Y_x^{(1)}(\mathbf{i}))_{x \geq 0})$ are i.i.d. for $\mathbf{i} \in \mathbb{T}$.

Figure 1. Cell division with multiplication of parasites, random sharing and contamination. Each parasite gives birth to a random number of light parasites and dark parasites. Light parasites go into the first daughter cell, dark parasites go into the second daughter cell and square parasites contaminate the cells from outside the cell population. But light/ dark/ square parasites then behave in the same way.



This model is a Markov chain indexed by a tree. This subject has been studied in the literature (see e.g. [5, 6, 9]) in the symmetric independent case. That is, $\forall(\mathbf{i}, k) \in \mathbb{T} \times \mathbb{N}$,

$$\mathbb{P}((Z_{\mathbf{i}0}, Z_{\mathbf{i}1}) = (k_0, k_1) \mid Z_{\mathbf{i}} = k) = \mathbb{P}(Z_{\mathbf{i}0} = k_0 \mid Z_{\mathbf{i}} = k) \mathbb{P}(Z_{\mathbf{i}1} = k_1 \mid Z_{\mathbf{i}} = k).$$

But this identity does not hold here since we are interested in unequal sharing of parasites. Guyon [12] proves limit theorems for a Markov chain indexed by a binary tree where asymmetry and dependence are allowed. His theorem is the key argument to prove the convergence of asymptotic proportions of cells with a given number of parasites here. Indeed, contamination ensures that the process which counts the number of parasites along the random walk on the binary tree of the cell population is ergodic and non trivial (see Section 5). This is the fundamental assumption to use Guyon's law of large numbers. Let us then introduce more precisely this process which gives the number of parasites in a random cell line.

Let $(a_i)_{i \in \mathbb{N}}$ be an i.i.d. sequence independent of $(Z_{\mathbf{i}})_{\mathbf{i} \in \mathbb{T}}$ such that

$$\mathbb{P}(a_1 = 0) = \mathbb{P}(a_1 = 1) = 1/2. \quad (2)$$

Denote by $f^{(0)}$ (resp $f^{(1)}$) the random p.g.f which gives the law of the size of the offspring of a parasite which goes in the first daughter cell (resp. in the second daughter cell):

$$f^{(0)}(s) := \mathbf{f}(s, 1) \quad \text{a.s.}, \quad f^{(1)}(t) := \mathbf{f}(1, t) \quad \text{a.s.}, \quad (s, t \in [0, 1]).$$

Let f be the mixed generating function of $f^{(0)}$ and $f^{(1)}$, i.e.

$$\mathbb{P}(f \in dg) = \frac{\mathbb{P}(f^{(0)} \in dg) + \mathbb{P}(f^{(1)} \in dg)}{2}.$$

Then $(Z_n)_{n \in \mathbb{N}} = (Z_{(a_1, a_2, \dots, a_n)})_{n \in \mathbb{N}}$ is a Branching Process in Random Environment with immigration depending on the state is zero or not: the reproduction law is given by its p.g.f f , the immigration law in zero is distributed as Y_0 , and the immigration law in $k \geq 1$ as Y_1 . Thus, we first need to prove asymptotic results for this process.

2 Main results

Galton Watson processes with immigration are well known (see e.g. [1, 18]). If the process is subcritical and the expectation of the logarithm of the immigration is finite, then it converges in distribution to a finite random variable. Otherwise it tends to infinity in probability. Key [13] has obtained the analogue result for Branching Processes in Random Environment with Immigration (IBPRE), in the subcritical case, with finite expectation of the logarithm. Actually he states results for multitype IBPRE, which have been complemented by Roitershtein [17] who obtained a strong law of large numbers and a central limit theorem for the partial sum.

In Section 4, we give the asymptotic behavior of IBPRE in the different cases, which means that we also consider the critical or supercritical case and the case when the expectation of the logarithm of the immigration is infinite. To get these results, we use some general statements on Markov processes (Section 3.2), classical arguments for Galton Watson process with immigration (see [18], which was inspired from [1]) and the tail of the time when IBPRE returns to 0 in the subcritical case, which is proved in [13].

We can then state results about branching processes in random environment $(Z_n)_{n \in \mathbb{N}}$ with immigration depending on the state is zero or not (Section 5) using coupling arguments and Section 3.2. This process gives the number of parasites along a random cell line. Recalling that immigration in state zero is distributed as Y_0 and immigration in state $k \geq 1$ is distributed as Y_1 , we prove the following expected result.

Theorem. (i) If $\mathbb{E}(\log(f'(1))) < 0$ and $\max(\mathbb{E}(\log^+(Y_i)) : i = 0, 1) < \infty$, then there exists a finite r.v. Z_∞ such that for every $k \in \mathbb{N}$, Z_n starting from k converges in distribution to Z_∞ as $n \rightarrow \infty$.

(ii) If $\mathbb{E}(\log(f'(1))) \geq 0$ or $\max(\mathbb{E}(\log^+(Y_i)) : i = 0, 1) = \infty$, then Z_n converges in probability to ∞ as $n \rightarrow \infty$.

With additional assumptions, we provide in Section 5 an estimate of the rate of convergence of $(Z_n)_{n \in \mathbb{N}}$ depending on the initial state.

Then, in Section 6, we prove asymptotic results on the population of cells in generation n as $n \rightarrow \infty$.

First, we consider the case when there is no contamination: $Y_0 = Y_1 = 0$ a.s. We determine when the organism recovers, meaning that the number of infected cells becomes negligible compared to the total number of cells. As stated in Proposition 2, the

recovery occurs a.s. iff $\mathbb{E}(\log(f'(1))) \leq 0$. Thus, we generalize results of Section 3 in [8] to random environment. Again, for any reproduction rate of parasites, we can find a necessary and sufficient condition on sharing of their offspring so that the organism recovers a.s.

As explained in introduction, a natural example is the random binomial repartition of parasites. If the reproduction of parasites is given by the r.v. Z and the random parameter of the binomial repartition is given $P \in [0, 1]$, the a.s. recovery criterion becomes

$$\log(\mathbb{E}(Z)) \leq \mathbb{E}(\log(1/P)).$$

Second we take into account the contamination by parasites from outside the cell population with assumptions (1). We focus on proportions of cells in generation n with a given number of parasites:

$$F_k(n) := \frac{\#\{\mathbf{i} \in \mathbb{G}_n : Z_{\mathbf{i}} = k\}}{2^n} \quad (k \in \mathbb{N}).$$

Using [12] and the theorem above, we prove the following law of large numbers.

Theorem. *If $\mathbb{E}(\log(f'(1))) < 0$ and $\max(\mathbb{E}(\log^+(Y_i)) : i = 0, 1) < \infty$, then for every $k \in \mathbb{N}$, $F_k(n)$ converges in probability to a deterministic number f_k as $n \rightarrow \infty$, such that $f_0 > 0$ and $\sum_{k=0}^{\infty} f_k = 1$. Otherwise, for every $k \in \mathbb{N}$, $F_k(n)$ converges in probability to 0 as $n \rightarrow \infty$.*

Finally, in Section 7, we give the asymptotic behavior of the total number of parasites in generation n in the case when the growth of parasites follows a Galton Watson process and the contamination does not depend on the state of cell.

3 Preliminaries

We recall first some results about Branching Processes in Random Environment (BPRE) and then about Markov chains, which will be both useful to study BPRE with immigration $(Z_n)_{n \in \mathbb{N}}$. Recall that we denote by k the initial number of parasites and by \mathbb{P}_k the probability associated with.

3.1 Branching Processes in Random Environment (BPRE)

We consider here a BPRE $(Z_n)_{n \in \mathbb{N}}$ specified by a sequence of i.i.d. generating functions $(f_n)_{n \in \mathbb{N}}$ distributed as f [2, 3, 19]. More precisely, conditionally on the environment $(f_n)_{n \in \mathbb{N}}$, particles at generation n reproduce independently of each other and their offspring has generating function f_n . Then Z_n is the number of particles at generation n and Z_{n+1} is the sum of Z_n independent random variables with generating function f_n . That is, for every $n \in \mathbb{N}$,

$$\mathbb{E}(s^{Z_{n+1}} | Z_0, \dots, Z_n; f_0, \dots, f_n) = f_n(s)^{Z_n} \quad (0 \leq s \leq 1).$$

Thus, denoting by $F_n := f_0 \circ \dots \circ f_{n-1}$, we have for every $k \in \mathbb{N}$,

$$\mathbb{E}_k(s^{Z_{n+1}} | f_0, \dots, f_n) = \mathbb{E}(s^{Z_{n+1}} | Z_0 = k, f_0, \dots, f_n) = F_n(s)^k \quad (0 \leq s \leq 1).$$

When the environments are deterministic (i.e. f is a deterministic generating function), this process is the Galton Watson process with reproduction law N , where f is the generating function of N .

The process $(Z_n)_{n \in \mathbb{N}}$ is called subcritical, critical or supercritical if

$$\mathbb{E}(\log(f'(1)))$$

is negative, zero or positive respectively. This process becomes extinct a.s.:

$$\mathbb{P}(\exists n \in \mathbb{N} : Z_n = 0) = 1$$

iff it is subcritical or critical [2] (see [10] for finer results).

In the critical case, we make the following integrability assumption:

$$0 < \mathbb{E}(\log(f'_0(1))^2) < \infty, \quad \mathbb{E}([1 + \log(f'_0(1))]f''_0(1)/2f'_0(1)) < \infty,$$

so that there exist $0 < c_1 < c_2 < \infty$ such that for every $n \in \mathbb{N}$ (see [16])

$$c_1/\sqrt{n} \leq \mathbb{P}(Z_n > 0) \leq c_2/\sqrt{n}. \quad (3)$$

See [7] for more general result in the critical case.

3.2 Markov chains

We consider now a Markov chain $(Z_n)_{n \in \mathbb{N}}$ taking values in \mathbb{N} and introduce the first time T_0 when $(Z_n)_{n \in \mathbb{N}}$ visits 0 after time 0:

$$T_0 := \inf\{i > 0 : Z_i = 0\}.$$

Denote by

$$u_n := \mathbb{P}_0(Z_n = 0), \quad u_\infty := 1/\mathbb{E}_0(T_0) \quad (1/\infty = 0).$$

By now, we assume $0 < \mathbb{P}_0(Z_1 = 0) < 1$ and we give the asymptotic behavior of $(Z_n)_{n \in \mathbb{N}}$. The first part of (i) is the classical ergodic property for an aperiodic positive recurrent Markov chain and we provide an estimate of the speed of convergence depending on the initial state. Then (ii) gives the null recurrent case, which is also a classical result.

Lemma 1. (i) *If for every $k \in \mathbb{N}$, $\mathbb{E}_k(T_0) < \infty$, then Z_n starting from k converges in distribution to a finite random variable Z_∞ , which does not depend on k and verifies*

$$\mathbb{P}(Z_\infty = 0) > 0.$$

Moreover there exists $A > 0$ such that for all $n, k \in \mathbb{N}$,

$$\begin{aligned} & \sum_{l \in \mathbb{N}} |\mathbb{P}_k(Z_n = l) - \mathbb{P}(Z_\infty = l)| \\ & \leq A \left[\sup_{n/2 \leq l \leq n} \{|u_l - u_\infty|\} + \mathbb{E}_0(T_0 \mathbb{1}_{T_0 > n/4}) + \mathbb{E}_k(T_0 \mathbb{1}_{T_0 > n/4}) \right]. \end{aligned} \quad (4)$$

(ii) *If $\mathbb{E}_0(T_0) = \infty$ and for every $l \in \mathbb{N}$, $\mathbb{P}_l(T_0 < \infty) > 0$, then for every $k \in \mathbb{N}$, $Z_n \rightarrow \infty$ in \mathbb{P}_k -probability as $n \rightarrow \infty$.*

Proof of (i). First, note that by the Markov property, for every $n \in \mathbb{N}$,

$$\begin{aligned}
& |\mathbb{P}_k(Z_n = 0) - u_\infty| \\
&= \left| \sum_{j=1}^n \mathbb{P}_k(T_0 = j) \mathbb{P}_0(Z_{n-j} = 0) - u_\infty \right| \\
&\leq \sum_{j=1}^n \mathbb{P}_k(T_0 = j) |u_{n-j} - u_\infty| + u_\infty \mathbb{P}_k(T_0 > n).
\end{aligned} \tag{5}$$

On the event $\{T_0 \leq n\}$, define R_n as the last passage time of $(Z_n)_{n \in \mathbb{N}}$ by 0 before time n :

$$R_n := \sup\{i \leq n : Z_i = 0\}.$$

For all $0 \leq i \leq n$ and $l \in \mathbb{N}$, by the Markov property,

$$\begin{aligned}
\mathbb{P}_k(Z_n = l) &= \mathbb{P}_k(T_0 > n, Z_n = l) + \sum_{i=0}^n \mathbb{P}_k(T_0 \leq n, R_n = n - i, Z_n = l) \\
&= \mathbb{P}_k(T_0 > n, Z_n = l) + \sum_{i=0}^n \mathbb{P}_k(Z_{n-i} = 0) \mathbb{P}_0(Z_i = l, T_0 > i).
\end{aligned}$$

Define now

$$\alpha_l := u_\infty \sum_{i=0}^{\infty} \mathbb{P}_0(Z_i = l, T_0 > i).$$

We then have

$$\begin{aligned}
|\mathbb{P}_k(Z_n = l) - \alpha_l| &\leq \mathbb{P}_k(T_0 > n, Z_n = l) + u_\infty \sum_{i=n+1}^{\infty} \mathbb{P}(Z_i = l, T_0 > i) \\
&\quad + \sum_{i=0}^n \mathbb{P}(Z_i = l, T_0 > i) |u_\infty - \mathbb{P}_k(Z_{n-i} = 0)|.
\end{aligned}$$

Summing over l leads to

$$\begin{aligned}
\sum_{l \in \mathbb{N}} |\mathbb{P}_k(Z_n = l) - \alpha_l| &\leq \mathbb{P}_k(T_0 > n) + u_\infty \mathbb{E}_0(T_0 \mathbb{1}_{T_0 > n+1}) \\
&\quad + \sum_{i=0}^n \mathbb{P}(T_0 > i) |u_\infty - \mathbb{P}_k(Z_{n-i} = 0)|.
\end{aligned} \tag{6}$$

Moreover using (5), we have for all $0 \leq n_0 \leq n$,

$$\begin{aligned}
& \sum_{i=0}^n \mathbb{P}(T_0 > i) |u_\infty - \mathbb{P}_k(Z_{n-i} = 0)| \\
&\leq \sum_{i=0}^n \mathbb{P}_0(T_0 > i) \left[\sum_{j=1}^{n-i} \mathbb{P}_k(T_0 = j) |u_{n-i-j} - u_\infty| + u_\infty \mathbb{P}_k(T_0 > n-i) \right] \\
&\leq \sum_{i=0}^n \mathbb{P}_0(T_0 > i) \sum_{j=1}^{n-i} \mathbb{P}_k(T_0 = j) |u_{n-i-j} - u_\infty| + u_\infty \sum_{i=0}^n \mathbb{P}_0(T_0 > i) \mathbb{P}_k(T_0 > n-i) \tag{7}
\end{aligned}$$

Finally, denoting by $M := \sup_{n \in \mathbb{N}} \{|u_n - u_\infty|\}$,

$$\begin{aligned}
& \sum_{i=0}^n \mathbb{P}_0(T_0 > i) \sum_{j=1}^{n-i} \mathbb{P}_k(T_0 = j) |u_{n-i-j} - u_\infty| \\
& \leq \sup_{n_0 \leq l \leq n} \{|u_l - u_\infty|\} \sum_{i=0}^n \mathbb{P}_0(T_0 > i) \sum_{j=1}^{n-i} \mathbb{P}_k(T_0 = j) 1_{n-i-j \geq n_0} \\
& \quad + M \sum_{i=0}^n \mathbb{P}_0(T_0 > i) \sum_{j=1}^{n-i} \mathbb{P}_k(T_0 = j) 1_{n-i-j < n_0} \\
& \leq \sup_{n_0 \leq l \leq n} \{|u_l - u_\infty|\} \sum_{i=0}^n \mathbb{P}_0(T_0 > i) \sum_{j=1}^{n-i} \mathbb{P}_k(T_0 = j) \\
& \quad + M \sum_{i=0}^{n-n_0} \mathbb{P}_0(T_0 > i) \mathbb{P}_k(T_0 > n - n_0 - i). \tag{8}
\end{aligned}$$

Combining (6), (7) and (8) and using that

$$\begin{aligned}
& \sum_{i=0}^n \mathbb{P}_0(T_0 > i) \mathbb{P}_k(T_0 > n - i) \leq \mathbb{E}_0(T_0 \mathbb{1}_{T_0 > n/2}) + \mathbb{E}_k(T_0 \mathbb{1}_{T_0 > n/2}), \\
& \sum_{i=0}^{n-n_0} \mathbb{P}_0(T_0 > i) \mathbb{P}_k(T_0 \geq n - n_0 - i) \leq \mathbb{E}_0(T_0 \mathbb{1}_{T_0 > (n-n_0)/2}) + \mathbb{E}_k(T_0 \mathbb{1}_{T_0 > (n-n_0)/2}),
\end{aligned}$$

we get, for all $0 \leq n_0 \leq n$,

$$\begin{aligned}
\sum_{l \in \mathbb{N}} |\mathbb{P}_k(Z_n = l) - \alpha_l| & \leq \mathbb{P}_k(T_0 > n) + u_\infty \mathbb{E}_0(T_0 \mathbb{1}_{T_0 > n+1}) + \sup_{n_0 \leq l \leq n} \{|u_l - u_\infty|\} \mathbb{E}_0(T_0) \\
& \quad + [u_\infty + M] [\mathbb{E}_0(T_0 \mathbb{1}_{T_0 > (n-n_0)/2}) + \mathbb{E}_k(T_0 \mathbb{1}_{T_0 > (n-n_0)/2})]. \tag{9}
\end{aligned}$$

As $\mathbb{P}_0(Z_1 = 0) > 0$, by the renewal theorem [11], $u_n \xrightarrow{n \rightarrow \infty} u_\infty$. Adding that $\mathbb{E}_k(T_0) < \infty$ and $\mathbb{E}_0(T_0) < \infty$ ensures that

$$\sum_{l \in \mathbb{N}} |\mathbb{P}_k(Z_n = l) - \alpha_l| \xrightarrow{n \rightarrow \infty} 0,$$

which proves that Z_n starting from k converges in distribution to a r.v. Z_∞ which does not depend on k .

The inequality of (i) is obtained by letting $n_0 = n/2$ in (9). \square

Proof of (ii). If $\mathbb{E}_0(T_0) = \infty$, then by the renewal theorem again [11],

$$u_n \xrightarrow{n \rightarrow \infty} 0.$$

So

$$D_n = \inf\{k - n : k \geq n, Z_k = 0\} \xrightarrow{n \rightarrow \infty} \infty, \quad \text{in probability.}$$

Assume that there exist $l \in \mathbb{N}$, $\epsilon > 0$ and an increasing sequence of integers $(u_n)_{n \in \mathbb{N}}$ such that

$$\mathbb{P}_k(Z_{u_n} = l) \geq \epsilon.$$

As $\mathbb{P}_l(T_0 < \infty) > 0$ by hypothesis, there exists $N > 0$ such that

$$\mathbb{P}_l(T_0 = N) > 0.$$

Thus, by the Markov property,

$$\mathbb{P}_k(Z_{u_n+K} = 0) \geq \mathbb{P}_k(Z_{u_n} = l) \mathbb{P}_l(T_0 = N) \geq \epsilon \mathbb{P}_l(T_0 = N).$$

Then, for all $n \in \mathbb{N}$,

$$\mathbb{P}_k(D_{u_n} \leq N) \geq \epsilon \mathbb{P}_l(T_0 = N) > 0,$$

which is in contradiction with the fact that $D_n \rightarrow \infty$ in \mathbb{P}_k as $n \rightarrow \infty$. Then, $\mathbb{P}_k(Z_n = l) \rightarrow 0$ as $n \rightarrow \infty$. \square

4 Branching processes in random environment with immigration (IBPRE)

We consider here a BPRE $(Z_n)_{n \in \mathbb{N}}$ whose reproduction law is given by the random p.g.f f and we add at each generation $n + 1$ a random number of immigrants Y_n independent and identically distributed as a r.v Y such that

$$\mathbb{P}(Y = 0) > 0.$$

More precisely, for every $n \in \mathbb{N}$,

$$Z_{n+1} = Y_n + \sum_{i=1}^{Z_n} X_i, \tag{10}$$

where $(X_i)_{i \in \mathbb{N}}$, Y_n and Z_n are independent and conditionally on $f_n = g$, the $(X_i)_{i \in \mathbb{N}}$ are i.i.d. with common probability generating function g .

Note that if the contamination does not depend on the fact that this cell is already infected or not (i.e. Y_0 and Y_1 are identically distributed), then the number of parasites in a random cell line defined in Introduction is a IBPRE whose reproduction law given by f and immigration by $Y \stackrel{d}{=} Y_0 \stackrel{d}{=} Y_1$.

We give now the asymptotic behavior of this process. These results are classical for the Galton Watson process with immigration [1, 18]. We follow the same method in the case of random environment for the subcritical and supercritical cases. We give in (ii) the tail of the time

$$T_0 = \inf\{n > 0 : Z_n = 0\}$$

when the process returns to 0 in the subcritical case, which is proved in [13] and we use Section 3.2 for the critical case.

Proposition 1. (i) If $\mathbb{E}(\log(f'(1))) < 0$ and $\mathbb{E}(\log^+(Y)) < \infty$, then Z_n converges in distribution to a finite random variable as $n \rightarrow \infty$ and $\lim_{n \rightarrow \infty} \mathbb{P}(Z_n = 0) > 0$. Otherwise $Z_n \rightarrow \infty$ as $n \rightarrow \infty$.

(ii) If $\mathbb{E}(\log(f'(1))) < 0$ and there exists $q > 0$ such that $\mathbb{E}(Y^q) < \infty$, then there exist $c, d > 0$ such that for every $n \in \mathbb{N}$,

$$\mathbb{P}(T_0 > n) \leq ce^{-dn}.$$

(iii) Assume $\mathbb{E}(f'(1)^{-1}) < 1$ and $\mathbb{E}(\log^+(Y)) < \infty$, then there exists a finite r.v. W such that

$$[\prod_{i=0}^{n-1} f'_i(1)]^{-1} Z_n \xrightarrow{n \rightarrow \infty} W, \quad \text{in } \mathbb{P}.$$

Note also that by the Borel-Cantelli lemma, if $\mathbb{E}(\log^+(Y_1)) = \infty$, then for every $c > 1$,

$$\limsup_{n \rightarrow \infty} c^{-n} Z_n = \infty \quad \text{a.s.}$$

since $Z_n \geq Y_n$ a.s. Moreover the proof of Section 5 provides an other approach to prove that $(Z_n)_{n \in \mathbb{N}}$ tends to ∞ if $\mathbb{E}(\log^+(Y)) = \infty$.

Proof of (i) and (ii) in the subcritical case: $\mathbb{E}(\log(f'(1))) < 0$. The subcritical case with assumption $\mathbb{E}(\log^+(Y)) < \infty$ is handled in [13]: First part of (i) is Theorem 3.3 and (ii) is a consequence of Theorem 4.2 of [13].

We focus now on the case $\mathbb{E}(\log^+(Y)) = \infty$ and prove that Z_n converges in probability to ∞ . The proof is close to the Galton Watson case (see [1] or [18]). First, by Borel-Cantelli lemma,

$$\limsup_{k \rightarrow \infty} \log^+(Y_k)/k = \infty \quad \text{a.s.}$$

Then, for every $c \in (0, 1)$,

$$\limsup_{k \rightarrow \infty} c^k Y_k = \infty \quad \text{a.s.} \tag{11}$$

Note that

$$Z_n = \sum_{k=0}^{n-1} Z_{k,n},$$

where $Z_{k,n}$ is the number of descendants in generation n of immigrants in generation $n - k$. Thus, denoting by $Y_{k,n}$ the number of immigrants in generation $n - k$ and $X_i(k, n)$ the number of descendants in generation n of immigrant i in generation $n - k$, we have

$$Z_n = \sum_{k=0}^{n-1} \sum_{i=1}^{Y_{k,n}} X_i(k, n).$$

This sum increases stochastically as n tends to infinity and converges in distribution to

$$Z_\infty = \sum_{k=0}^{\infty} \sum_{i=1}^{Y_k} X_i(k),$$

where conditionally on $(f_i : i \in \mathbb{N})$, $(X_i(k) : i \in \mathbb{N}, k \in \mathbb{N})$ are independent and the probability generating function of $X_i(k)$ is equal to $f_{k-1} \circ \dots \circ f_0$. Roughly speaking, $X_i(k)$ is the contribution of immigrant i which arrives k generations before 'final time' ∞ . The integer $X_i(k)$ is the population in generation k of a BPPE without immigration starting from 1.

Assume now that $Z_\infty < \infty$ with a positive probability. As $(X_i(k) : k \in \mathbb{N}, 1 \leq i \leq Y_k)$ are integers, then conditionally on $Z_\infty < \infty$, only a finite number of them are positive. Thus, by Borel-Cantelli lemma, conditionally on $(Z_\infty < \infty, Y_k : k \in \mathbb{N}, f_i : i \in \mathbb{N})$,

$$\sum_{k=0}^{\infty} Y_k \mathbb{P}(X_1(k) > 0) < \infty \quad \text{a.s.}$$

Moreover, by convexity, for all g p.g.f and $s \in [0, 1]$,

$$\frac{1 - g(s)}{1 - s} = \frac{g(1) - g(s)}{1 - s} \geq \frac{g(1) - g(0)}{1 - 0} = 1 - g(0), \quad (0 \leq s \leq 1).$$

Then $1 - g(s) \geq (1 - g(0))(1 - s)$ and by induction, we have for every $k \in \mathbb{N}$,

$$\begin{aligned} \mathbb{P}(X_1(k) > 0 \mid f_i : i \in \mathbb{N}) &= 1 - f_{k-1} \circ \dots \circ f_0(0) \\ &\geq \prod_{i=0}^{k-1} (1 - f_i(0)) \\ &= \exp(S_k), \end{aligned}$$

where $S_k := \sum_{i=0}^{k-1} \log(1 - f_i(0))$. Thus, conditionally on $(Z_\infty < \infty, Y_k : k \in \mathbb{N}, f_i : i \in \mathbb{N})$,

$$\sum_{k=0}^{\infty} Y_k \exp(S_k) < \infty \quad \text{a.s.}$$

Thus, on the event $\{Z_\infty < \infty\}$ which has a positive probability, we get

$$\sum_{k=0}^{\infty} Y_k \exp(S_k) < \infty \quad \text{a.s.}$$

Moreover S_n is a random walk with negative drift $\mathbb{E}(\log(1 - f_0(0)))$. So letting $\alpha < \mathbb{E}(\log(1 - f_0(0)))$, $\mathbb{P}(S_n < \alpha n)$ decreases exponentially by classical large deviation results. Then by Borel-Cantelli lemma, S_n is less than αn for a finite number of n , and

$$L := \inf_{n \in \mathbb{N}} \{S_n - \alpha n\} > -\infty \quad \text{a.s.}$$

Using that for every $k \in \mathbb{N}$, $S_k \geq \alpha k + L$ a.s., we get

$$\sum_{k=0}^{\infty} \exp(\alpha k) Y_k < \infty,$$

with positive probability. This is in contradiction with (11). Then $Z_\infty = \infty$ a.s. and Z_n converges in probability to ∞ as $n \rightarrow \infty$. \square

Proof of (i) in the critical and supercritical case: $\mathbb{E}(\log(f'(1))) \geq 0$. First, we focus on the critical case. Recall that $T_0 = \inf\{i > 0 : Z_i = 0\}$ and consider $(\bar{Z}_n)_{n \in \mathbb{N}}$ the BPRE associated with $(Z_n)_{n \in \mathbb{N}}$, that is the critical BPRE with reproduction law f and no immigration. Thanks to (3), there exists $c_1 > 0$ such that for ever $n \in \mathbb{N}$,

$$\mathbb{P}_1(\bar{Z}_n > 0) \geq c_1/\sqrt{n}.$$

Adding that

$$\mathbb{P}_1(T_0 > n) = \mathbb{P}_1(Z_n > 0) \geq \mathbb{P}_1(\bar{Z}_n > 0),$$

ensures that

$$\mathbb{E}_1(T_0) = \infty.$$

Then $\mathbb{E}_0(T_0) = \infty$ since IBPRE $(Z_n)_{n \in \mathbb{N}}$ starting from 1 is stochastically larger than $(Z_n)_{n \in \mathbb{N}}$ starting from 0. Moreover $\forall k \in \mathbb{N}$, $\mathbb{P}_k(T_0 < \infty) > 0$, since $\mathbb{P}_k(\bar{T}_0 < \infty) = 1$ and $\mathbb{P}(Y = 0) > 0$. Then Lemma 1 (ii) ensures that $Z_n \rightarrow \infty$ in \mathbb{P} as $n \rightarrow \infty$.

For the supercritical case, follow the proof in the critical case (or use the result with a coupling argument) to get that $Z_n \rightarrow \infty$ in probability as $n \rightarrow \infty$ \square

Proof of (iii). We follow again [18]. If $\mathbb{E}(\log^+(Y)) < \infty$, by Borel-Cantelli Lemma

$$\limsup_{k \rightarrow \infty} \log^+(Y_k)/k = 0.$$

Then for every $c > 1$,

$$\sum_{k=0}^{\infty} c^{-k} Y_k < \infty \quad \text{a.s.} \quad (12)$$

Define

$$P_n := [\Pi_{i=0}^{n-1} f'_i(1)]^{-1},$$

and denote by \mathcal{F}_n the σ -field generated by $(Z_i : 0 \leq i \leq n)$, $(P_i : 0 \leq i \leq n)$ and $(Y_k : k \in \mathbb{N})$. Then using (10), we have

$$\begin{aligned} \mathbb{E}(P_{n+1}Z_{n+1} \mid \mathcal{F}_n) &= \mathbb{E}(P_{n+1}[\sum_{i=1}^{Z_n} X_i + Y_n] \mid \mathcal{F}_n) \\ &= P_n \mathbb{E}(f'_n(1)^{-1} \sum_{i=1}^{Z_n} X_i \mid \mathcal{F}_n) + P_n \mathbb{E}(f'(1)^{-1}) Y_n \\ &= P_n \mathbb{E}(f'_n(1)^{-1} Z_n \mathbb{E}(X_1 \mid f_n) \mid \mathcal{F}_n) + P_n \mathbb{E}(f'(1)^{-1}) Y_n \\ &= P_n Z_n + P_n \mathbb{E}(f'(1)^{-1}) Y_n. \end{aligned}$$

So $P_n Z_n$ is a submartingale. Moreover

$$\mathbb{E}(P_n Z_n \mid \mathcal{F}_0) = Z_0 + \sum_{i=0}^{n-1} \mathbb{E}(f'(1)^{-1})^{i+1} Y_i.$$

By (12), if $\mathbb{E}(f'(1)^{-1}) < 1$, $P_n Z_n$ has bounded expectations and then converges a.s. to a finite r.v. \square

5 Ergodicity and convergence for a random cell line

Recall that $(Z_n)_{n \in \mathbb{N}}$ defined in Introduction is the number of parasites in a random cell line. The Markov chain $(Z_n)_{n \in \mathbb{N}}$ is a BPRE with state dependent immigration. The reproduction law is given by the p.g.f f , immigration in state 0 is distributed as Y_0 and immigration in state $k \geq 1$ is distributed as Y_1 . More precisely, for every $n \in \mathbb{N}$, conditionally on $Z_n = x$,

$$Z_{n+1} = Y_x^{(n)} + \sum_{i=1}^x X_i^{(n)}, \quad \text{where}$$

- (i) $(X_i^{(n)})_{i \in \mathbb{N}}$ and $Y_x^{(n)}$ are independent.
- (ii) Conditionally on $f_n = g$, the $(X_i^{(n)})_{i \in \mathbb{N}}$ are i.i.d. with common probability generating function g .
- (iii) For all $x \geq 1$ and $n \in \mathbb{N}$, $Y_x^{(n)} \stackrel{d}{=} Y_1$.

We have the following results, which generalize those of the previous section to the case when immigration depends on whether the state is zero or not.

Theorem 1. (i) If $\mathbb{E}(\log(f'(1))) < 0$ and $\max(\mathbb{E}(\log^+(Y_i)) : i = 0, 1) < \infty$, then there exists a finite random variable Z_∞ such that for every $k \in \mathbb{N}$, Z_n starting from k converges in distribution to Z_∞ as $n \rightarrow \infty$.

Moreover, if there exists $q > 0$ such that $\max(\mathbb{E}(Y_i^q) : i = 0, 1) < \infty$, then for every $\epsilon > 0$, there exist $0 < r < 1$ and $C > 0$ such that for all $n \in \mathbb{N}$ and $k \in \mathbb{N}$,

$$\sum_{l=0}^{\infty} |\mathbb{P}_k(Z_n = l) - \mathbb{P}(Z_\infty = l)| \leq C k^\epsilon r^n.$$

(ii) If $\mathbb{E}(\log(f'(1))) \geq 0$ or $\max(\mathbb{E}(\log^+(Y_i)) : i = 0, 1) = \infty$, Z_n converges in probability to infinity as $n \rightarrow \infty$.

Note again that by Borel-Cantelli lemma, if $\mathbb{E}(\log^+(Y_1)) = \infty$, then for every $c > 1$,

$$\limsup_{n \rightarrow \infty} c^{-n} Z_n = \infty \quad \text{a.s.},$$

since $Z_n \geq Y_n$ a.s.

The proof of (ii) in the critical or supercritical case ($\mathbb{E}(\log(f'(1))) \geq 0$) is directly derived from Proposition 1 and we focus now on the subcritical case:

$$\mathbb{E}(\log(f'(1))) < 0.$$

Recall that T_0 is the first time after 0 when $(Z_n)_{n \in \mathbb{N}}$ visits 0. Using IBPRE (see Section 4), we prove the following result in the subcritical case.

Lemma 2. *If $\max(\mathbb{E}(\log^+(Y_i)) : i = 0, 1) < \infty$, then for every $k \in \mathbb{N}$, $\mathbb{P}_k(T_0 < \infty) = 1$ and*

$$\sup_{n \in \mathbb{N}} \{\mathbb{P}_k(Z_n \geq l)\} \xrightarrow{l \rightarrow \infty} 0.$$

Moreover if there exists $q > 0$ such that $\max(\mathbb{E}(Y_i^q) : i = 0, 1) < \infty$, then for every $\epsilon > 0$, there exist $r > 0$ and $C > 0$ such that for all $n \in \mathbb{N}$, $k \geq 1$:

$$\mathbb{P}_0(T_0 \geq n) \leq Cr^n, \quad \mathbb{P}_k(T_0 \geq n) \leq Ck^\epsilon r^n.$$

Proof. We couple $(Z_n)_{n \in \mathbb{N}}$ with an IBPRE $(\tilde{Z}_n)_{n \in \mathbb{N}}$ with reproduction law given by the random p.g.f f (such as $(Z_n)_{n \in \mathbb{N}}$) and immigration Y defined by

$$Y := \max(Y_0, Y_1, \tilde{Y}),$$

where Y_0 , Y_1 , and \tilde{Y} are independent and \tilde{Y} is defined by

$$\mathbb{P}(\tilde{Y} = 0) = 1/2; \quad \forall n \in \mathbb{N}^*, \quad \mathbb{P}(\tilde{Y} = n) = \alpha n^{-1-\epsilon}, \quad \alpha := [2 \sum_{i=1}^{\infty} i^{-1-\epsilon}]^{-1}.$$

Thus immigration Y for \tilde{Z}_n is stochastically larger than immigration for Z_n (whereas reproduction law is the same), so that coupling gives

$$\forall n \in \mathbb{N}, \quad Z_n \leq \tilde{Z}_n \quad \text{a.s.}$$

Moreover, \tilde{Z}_n is still subcritical. Recalling that $\min(\mathbb{P}(Y_i = 0) : i = 0, 1) > 0$, $\mathbb{P}(\tilde{Y} = 0) = 1/2$, and that the expectation of the logarithm of every r.v. is finite, we have

$$\mathbb{E}(\log^+(Y)) < \infty, \quad \mathbb{P}(Y = 0) > 0.$$

Then Proposition 1 (i) ensures that \tilde{Z}_n converges in distribution to a finite random variable, so that

$$\sup_{n \in \mathbb{N}} \{\mathbb{P}_k(Z_n \geq l)\} \leq \sup_{n \in \mathbb{N}} \{\mathbb{P}_k(\tilde{Z}_n \geq l)\} \xrightarrow{l \rightarrow \infty} 0.$$

Proposition 1 (i) ensures also that for every $k \in \mathbb{N}$, $\lim_{n \rightarrow \infty} \mathbb{P}_k(Z_n = 0) > 0$. Thus, for every $k \in \mathbb{N}$, $\mathbb{P}_k(\tilde{T}_0 < \infty) = 1$ and then $\mathbb{P}_k(T_0 < \infty) = 1$. This completes the first part of the lemma.

We assume now that there exists $q > 0$ such that $\max(\mathbb{E}(Y_i^q) : i = 0, 1) < \infty$. Moreover $\mathbb{E}(\tilde{Y}^{\epsilon/2}) < \infty$, so letting $q' = \min(\epsilon/2, q)$, we have

$$\mathbb{E}(Y^{q'}) < \infty.$$

We can then apply Proposition 1 (ii) to IBPRE $(\tilde{Z}_n)_{n \in \mathbb{N}}$, so that there exist $c, d > 0$ such that for every $n \in \mathbb{N}$,

$$\mathbb{P}_0(\tilde{T}_0 > n) \leq ce^{-dn}.$$

Recalling that for all $k, n \in \mathbb{N}$,

$$\mathbb{P}_k(T_0 \geq n) \leq \mathbb{P}_k(\tilde{T}_0 \geq n),$$

we get $\mathbb{P}_0(T_0 \geq n) \leq ce^{-dn}$. Moreover for every $k \in \mathbb{N}$,

$$\mathbb{P}_0(\widetilde{T}_0 > n) \geq \mathbb{P}(Y \geq k)\mathbb{P}_k(\widetilde{T}_0 \geq n).$$

By definition of Y , there exists $\beta > 0$ such that for every $n \in \mathbb{N}$,

$$\mathbb{P}(Y \geq n) \geq \beta n^{-\epsilon}.$$

Using these inequalities gives

$$\mathbb{P}_k(T_0 \geq n) \leq \mathbb{P}_k(\widetilde{T}_0 \geq n) \leq \beta^{-1}k^\epsilon \mathbb{P}_0(\widetilde{T}_0 > n) \leq \beta^{-1}ck^\epsilon e^{-dn}.$$

This completes the proof. \square

Proof of Theorem 1 (i) and (ii) in the subcritical case: $\mathbb{E}(\log(f'(1))) < 0$. We split the proof into 4 cases:

CASE 1: $\max(\mathbb{E}(\log^+(Y_i)) : i = 0, 1) < \infty$.

CASE 2: There exists $q > 0$ such that $\max(\mathbb{E}(Y_i^q) : i = 0, 1) < \infty$.

CASE 3: $\mathbb{E}(\log^+(Y_1)) = \infty$.

CASE 4: $\mathbb{E}(\log^+(Y_0)) = \infty$.

First, note that $\mathbb{P}(Y_0 = 0) > 0$ ensures that $\mathbb{P}_0(Z_1 = 0) > 0$ and we can use results of Section 3.2.

CASE 1. In this case, by Lemma 2, $(Z_n)_{n \in \mathbb{N}}$ is bounded in distribution:

$$\sup_{n \in \mathbb{N}} \{\mathbb{P}_0(Z_n \geq l)\} \xrightarrow{l \rightarrow \infty} 0.$$

If $\mathbb{E}_0(T_0) = \infty$, then $Z_n \rightarrow \infty$ in \mathbb{P}_0 by Lemma 1 (ii), which is in contradiction with the previous limit.

Then $\mathbb{E}_0(T_0) < \infty$. We prove now that $\forall k \geq 1$, $\mathbb{E}_k(T_0) < \infty$ by a coupling argument. Let $k \geq 1$ and change only immigration to get a Markov process $(\widetilde{Z}_n)_{n \in \mathbb{N}}$ which is larger than $(Z_n)_{n \in \mathbb{N}}$:

$$\forall n \in \mathbb{N}, \quad \widetilde{Z}_n \geq Z_n \text{ a.s.}$$

Its immigrations \widetilde{Y}_0 and \widetilde{Y}_1 satisfy

$$\widetilde{Y}_1 \stackrel{d}{=} Y_1, \quad \forall n \in \mathbb{N}, \quad \mathbb{P}(\widetilde{Y}_0 \geq n) \geq \mathbb{P}(Y_0 \geq n),$$

$$\mathbb{P}(\widetilde{Y}_0 \geq k) > 0, \quad \max(\mathbb{E}(\log(\widetilde{Y}_i)) : i = 0, 1) < \infty.$$

Then, we have again $\mathbb{E}_0(\widetilde{T}_0) < \infty$, which entails that $\mathbb{E}_k(\widetilde{T}_0) < \infty$ since $\mathbb{P}(\widetilde{Y}_0 \geq k) > 0$. As for every $n \in \mathbb{N}$, $\widetilde{Z}_n \geq Z_n$ a.s., we have

$$\mathbb{E}_k(T_0) \leq \mathbb{E}_k(\widetilde{T}_0) < \infty.$$

Then Lemma 1 (i) ensures that for every $k \in \mathbb{N}$, $(Z_n)_{n \in \mathbb{N}}$ converges in distribution to a finite random variable Z_∞ , which does not depend on k and verifies $\mathbb{P}(Z_\infty = 0) > 0$.

CASE 2: By Lemma 1 (i), we have

$$\sum_{l \in \mathbb{N}} |\mathbb{P}_k(Z_n = l) - \mathbb{P}(Z_\infty = l)| \leq A \left[\sup_{n/2 \leq l \leq n} \{|u_l - u_\infty|\} + \mathbb{E}_0(T_0 \mathbb{1}_{T_0 > n/4}) + \mathbb{E}_k(T_0 \mathbb{1}_{T_0 > n/4}) \right]. \quad (13)$$

Moreover by Lemma 2, for every $\epsilon > 0$, there exists $C > 0$ such that

$$\mathbb{P}_k(T_0 \geq n) \leq Ck^\epsilon r^n, \quad \mathbb{P}_0(T_0 \geq n) \leq Cr^n. \quad (14)$$

So for every $r' \in (r, 1)$, $\mathbb{E}_0(\exp(-\log(r)T_0)) < \infty$. Then, by Kendall renewal theorem [14], there exists $\rho \in (0, 1)$ and $c > 0$ such that for every $n \in \mathbb{N}$,

$$|u_n - u_\infty| \leq c\rho^n. \quad (15)$$

Finally, (14) ensures that there exists $D > 0$ such that for every $n \in \mathbb{N}$,

$$\begin{aligned} \mathbb{E}_0(T_0 \mathbb{1}_{T_0 > n/4}) &\leq Dnr^{n/4}, \\ \mathbb{E}_k(T_0 \mathbb{1}_{T_0 > n/4}) &\leq Dnk^\epsilon r^{n/4}. \end{aligned}$$

Combining these two inequalities with (13) and (15), we get

$$\sum_{l \in \mathbb{N}} |\mathbb{P}_k(Z_n = l) - \mathbb{P}(Z_\infty = l)| \leq A[c\rho^n + Dnr^{n/4} + Dnk^\epsilon r^{n/4}],$$

which ends the proof in CASE 2.

CASE 3. Change immigration of $(Z_n)_{n \in \mathbb{N}}$ to get an IBPRE $(\tilde{Z}_n)_{n \in \mathbb{N}}$ whose immigration is distributed as Y_1 and whose reproduction law is still given by f . Then Proposition 1 (i) and $\mathbb{E}(\log^+(Y_1)) = \infty$ ensures that $(\tilde{Z}_n)_{n \in \mathbb{N}}$ starting from 0 tends in distribution to ∞ .

Then Lemma 1 (i) entails that $\mathbb{E}_0(\tilde{T}_0) = \infty$, so that for every $k \geq 1$,

$$\mathbb{E}_k(\tilde{T}_0) \geq \mathbb{E}_0(\tilde{T}_0) = \infty,$$

since the IBPRE $(\tilde{Z}_n)_{n \in \mathbb{N}}$ starting from $k \geq 1$ is stochastically larger than $(\tilde{Z}_n)_{n \in \mathbb{N}}$ starting from 0.

Moreover, under \mathbb{P}_k , $(Z_n)_{n \in \mathbb{N}}$ is equal to $(\tilde{Z}_n)_{n \in \mathbb{N}}$ until time $T_0 = \tilde{T}_0$. So $\mathbb{E}_k(T_0) = \infty$. Let $k \geq 1$ such that $\mathbb{P}_0(Z_1 = k) > 0$, then $\mathbb{E}_0(T_0) \geq \mathbb{P}_0(Z_1 = k)\mathbb{E}_k(T_0 - 1)$. This entails that

$$\mathbb{E}_0(T_0) = \infty.$$

By Lemma 1 (ii), $(Z_n)_{n \in \mathbb{N}}$ starting from any $k \in \mathbb{N}$ tends to ∞ in probability.

CASE 4. Denote by

$$X_i := \mathbb{P}(Z_i > 0 \mid Z_{i-1} = 1, f_{i-1}), \quad (i \geq 1),$$

the survival probability in environment f_{i-1} and introduce the following random walk

$$S_n = \sum_{i=1}^n \log(X_i).$$

Then

$$\mathbb{P}_1(Z_n > 0 \mid (f_0, f_1, \dots, f_{n-1})) \geq \prod_{i=1}^n X_i = \exp(S_n) \quad \text{a.s.},$$

so that

$$\begin{aligned} \mathbb{P}_k(Z_n > 0 \mid (f_0, f_1, \dots, f_{n-1})) &= 1 - \mathbb{P}_k(Z_n = 0 \mid (f_0, f_1, \dots, f_{n-1})) \\ &= 1 - [1 - \mathbb{P}_1(Z_n > 0 \mid (f_0, f_1, \dots, f_{n-1}))]^k \\ &\geq 1 - [1 - \exp(S_n)]^k \quad \text{a.s.} \end{aligned}$$

Thus

$$\mathbb{P}_k(Z_n > 0) \geq \mathbb{E}(1 - [1 - \exp(S_n)]^k).$$

Using the Markov property we have

$$\begin{aligned} \mathbb{E}_0(T_0 + 1) &\geq \sum_{k=1}^{\infty} \mathbb{P}(Y_0 = k) \mathbb{E}_k(T_0) \\ &= \sum_{k=1}^{\infty} \mathbb{P}(Y_0 = k) \sum_{n=1}^{\infty} \mathbb{P}_k(T_0 \geq n) \\ &\geq \sum_{k=1}^{\infty} \mathbb{P}(Y_0 = k) \sum_{n=1}^{\infty} \mathbb{P}_k(Z_n > 0) \\ &\geq \sum_{k=1}^{\infty} \mathbb{P}(Y_0 = k) \sum_{n=1}^{\infty} \mathbb{E}(1 - [1 - \exp(S_n)]^k). \end{aligned}$$

Moreover for all $x \in [0, 1[$ and $k \geq 0$, $\exp(k \log(1 - x)) \leq \exp(-kx)$, and by the law of large numbers, S_n/n tends a.s. to $\mathbb{E}(X_1) < 0$ so that there exists $n_0 \geq 1$ such that for every $n \geq n_0$,

$$\mathbb{P}(S_n/n \geq 3\mathbb{E}(X_1)/2) \geq 1/2.$$

We get then

$$\begin{aligned} \mathbb{E}_0(T_0 + 1) &\geq \sum_{k=1}^{\infty} \mathbb{P}(Y_0 = k) \sum_{n=1}^{\infty} \mathbb{E}(1 - \exp(-k \exp(S_n))) \\ &\geq [1 - e^{-1}] \sum_{n=1}^{\infty} \sum_{k=1}^{\infty} \mathbb{P}(k \exp(S_n) \geq 1) \mathbb{P}(Y_0 = k) \\ &\geq [1 - e^{-1}] \sum_{n=n_0}^{\infty} \mathbb{P}(S_n/n \geq 3\mathbb{E}(X_1)/2) \sum_{k \geq \exp(-3n\mathbb{E}(X_1)/2)}^{\infty} \mathbb{P}(Y_0 = k) \\ &\geq 2^{-1} [1 - e^{-1}] \sum_{n=n_0}^{\infty} \mathbb{P}(Y_0 \geq \exp(-3n\mathbb{E}(X_1)/2)) \\ &\geq 2^{-1} [1 - e^{-1}] \sum_{n=n_0}^{\infty} \mathbb{P}(\beta \log(Y_0) \geq n), \end{aligned}$$

where $\beta := [-3\mathbb{E}(X_1)/2]^{-1} > 0$. Then $\mathbb{E}(\log(Y_0)) = \infty$ ensures that $\mathbb{E}_0(T_0 + 1) = \infty$, so

$$\mathbb{E}_0(T_0) = \infty.$$

Conclude that $(Z_n)_{n \in \mathbb{N}}$ tends to ∞ in \mathbb{P}_k using Lemma 1 (ii). \square

6 Asymptotics for proportions of cells with a given number of parasites

6.1 Asymptotics without contamination

Here there is no contamination, i.e. $Y_0 = Y_1 = 0$ a.s. and we determine when the organism recovers, meaning that the number of contaminated cells becomes negligible compared to the total number of cells. We get the same result as Theorem 1 in [8] for the more general model considered here. Denote by N_n the number of contaminated cells.

Proposition 2. $N_n/2^n$ decreases as n grows.

If $\mathbb{E}(\log(f'(1))) \leq 0$, then $N_n/2^n \rightarrow 0$ a.s. as $n \rightarrow \infty$.

Otherwise, $N_n/2^n \rightarrow 0$ as $n \rightarrow \infty$ iff all parasites die out, which happens with a probability less than 1.

Example. Consider the case of the random binomial repartition of parasites mentioned in Introduction. Let $Z \in \mathbb{N}$ be a r.v. and $(P_i)_{i \in \mathbb{T}}$ be an i.i.d. sequence distributed as a r.v. $P \in [0, 1]$, such that $P \stackrel{d}{=} 1 - P$. In every generation, each parasite gives birth independently to a random number of parasites distributed as Z . When the cell \mathbf{i} divides, conditionally on $P_i = p$, each parasite of the cell \mathbf{i} goes independently in the first daughter cell with probability p (or it goes in the second daughter cell, which happens with probability $1 - p$). Then,

$$\mathbb{P}(f'(1) \in dx) = \mathbb{P}(\mathbb{E}(Z)P \in dx).$$

Thus, the organism recovers a.s. (i.e. $N_n/2^n$ tends a.s. to 0) iff

$$\log(\mathbb{E}(Z)) \leq \mathbb{E}(\log(1/P)).$$

This is the same criteria in the case when the offspring of each parasite goes a.s. in the same daughter cell (there, p is the probability that this offspring goes in the first daughter cell.)

Proof. Note that $N_n/2^n$ decreases to L as $n \rightarrow \infty$, since one infected cell has at most two

daughter cells which are infected. Moreover, for every $n \in \mathbb{N}$,

$$\begin{aligned}
\mathbb{E}\left(\frac{N_n}{2^n}\right) &= \frac{\mathbb{E}(\sum_{i \in \mathbb{G}_n} \mathbb{1}_{Z_i > 0})}{2^n} \\
&= \sum_{\mathbf{i} \in \mathbb{G}_n} \frac{1}{2^n} \mathbb{E}(\mathbb{1}_{Z_{\mathbf{i}} > 0}) \\
&= \sum_{\mathbf{i} \in \mathbb{G}_n} \mathbb{P}((a_0, \dots, a_{n-1}) = \mathbf{i}) \mathbb{P}(Z_{\mathbf{i}} > 0) \\
&= \mathbb{P}(Z_n > 0).
\end{aligned}$$

If $\mathbb{E}(\log(f'(1))) \leq 0$ (subcritical or critical case), then $\mathbb{P}(Z_n > 0)$ tends to 0 as $n \rightarrow \infty$ (see Section 3.1). Thus, $\mathbb{E}(L) = 0$ and $N_n/2^n$ tends to 0 a.s. as $n \rightarrow \infty$.

If $\mathbb{E}(\log(f'(1))) > 0$ (supercritical case), then $\mathbb{P}(Z_n > 0)$ tends to a positive value, which is equal to $\mathbb{P}(L > 0)$. We complete the proof with the following lemma. \square

Let us prove the following zero one law, where P_n is the total number of parasites in generation n .

Lemma 3. *If $\mathbb{E}(\log(f'(1))) > 0$, then*

$$\left\{ \lim_{n \rightarrow \infty} N_n/2^n > 0 \right\} = \{ \forall n \in \mathbb{N} : P_n > 0 \} \quad a.s.$$

Proof. First, we prove that conditionally on non-extinction of parasites, for every $K \in \mathbb{N}$, there exists a.s. a generation n such that $N_n \geq K$. Letting $K \in \mathbb{N}$, we fix p as the first integer such that $2^p \geq K$. Then $q := \mathbb{P}_1(N_p \geq K) > 0$ since $\mathbb{P}(N_1 = 2) > 0$.

Either the number of infected cells in generation p is more than K , which happens with probability q , or we can choose in generation p an infected cell $\mathbf{i}(1)$, since parasites have not died out. Then, with probability larger than q , the number of infected cells in generation p of the subtree rooted in this cell $\mathbf{i}(1)$ contains more than K parasites. Note that this probability is exactly equal to q iff the infected cell $\mathbf{i}(1)$ contains one single parasite. Recursively, we find a.s. a generation n such that $N_n \geq K$.

Then, recalling that we still work conditionally on non-extinction of parasites, the stopping time $T := \inf\{n \in \mathbb{N} : N_n \geq K\} < \infty$ a.s. We now also condition by $T = n$ and $N_T = k$. We can then choose one parasite in every infected cell in generation n , which we label by $1 \leq i \leq k$ and we denote by $N_p^{(i)}$ the number of cells in generation $n+p$ infected by parasites whose ancestor in generation n is the parasite i . By branching property, the integers $(N_p^{(i)} : 1 \leq i \leq k)$ are i.i.d. and $N_p^{(i)}/2^p \rightarrow L^{(i)}$ as $p \rightarrow \infty$, where $(L^{(i)} : 1 \leq i \leq k)$ are independent and $\mathbb{P}(L^{(i)} > 0) = \mathbb{P}(L > 0) > 0$ for every $1 \leq i \leq k$. Using that

$$N_{n+p} \geq \sum_{i=1}^k N_p^{(i)} \quad a.s.,$$

and as $k \geq K$, we get

$$\lim_{p \rightarrow \infty} N_{n+p}/2^p \geq \max(L^{(i)} : 1 \leq i \leq K) \quad a.s.$$

As $\sup(L^{(i)} : i \in \mathbb{N}) = \infty$ a.s., letting $K \rightarrow \infty$ ensures that a.s. $N_p/2^p$ does not tend to 0. \square

6.2 Asymptotics with contamination in the case $\mathbb{E}(\log(f'(1))) < 0$ and $\max(\mathbb{E}(\log^+(Y_i)) : i = 0, 1) < \infty$.

Define $F_k(n)$ the proportion of cells with k parasites in generation n :

$$F_k(n) := \frac{\#\{\mathbf{i} \in \mathbb{G}_n : Z_{\mathbf{i}} = k\}}{2^n} \quad (k \in \mathbb{N}).$$

We introduce the Banach space $l^1(\mathbb{N})$ and the subset of frequencies $\mathbb{S}^1(\mathbb{N})$ which we endow with the norm $\|\cdot\|_1$ defined by:

$$l^1(\mathbb{N}) := \{(x_i)_{i \in \mathbb{N}} : \sum_{i=0}^{\infty} |x_i| < \infty\}, \quad \|(x_i)_{i \in \mathbb{N}}\|_1 = \sum_{i=0}^{\infty} |x_i|,$$

$$\mathbb{S}^1(\mathbb{N}) := \{(f_i)_{i \in \mathbb{N}} : \forall i \in \mathbb{N}, f_i \in \mathbb{R}^+, \sum_{i=0}^{\infty} f_i = 1\}.$$

The main argument here is the law of large number proved by Guyon [12] for asymmetric Markov chains indexed by a tree.

Theorem 2. *If $\mathbb{E}(\log(f'(1))) < 0$ and $\max(\mathbb{E}(\log^+(Y_i)) : i = 0, 1) < \infty$, then $(F_k(n))_{k \in \mathbb{N}}$ converges in probability in $\mathbb{S}^1(\mathbb{N})$ to a deterministic sequence $(f_k)_{k \in \mathbb{N}}$ as $n \rightarrow \infty$, such that $f_0 > 0$ and $\sum_{k=0}^{\infty} f_k = 1$. Moreover, for every $k \in \mathbb{N}$, $f_k = \mathbb{P}(Z_{\infty} = k)$.*

Proof. Recall that $(Z_{\mathbf{i}})_{\mathbf{i} \in \mathbb{T}}$ is a Markov chain indexed by a tree and we are in the framework of bifurcating Markov chain studied in [12]. Thanks to the ergodicity of the number of parasites in a random cell line proved in the previous section (Theorem 1 (i)), we can directly apply Theorem 8 in [12] to get the convergence of proportions of cells with a given number of parasites. \square

But it seems that we can't apply Theorem 14 or Corollary 15 in [12] to get a.s. convergence of proportions, because of the term k^e in estimation of Theorem 1. For examples, we refer to the previous proposition.

Using again [12], we can prove also a law of large numbers and a central limit theorem for the proportions of cells with given number of parasites before generation n . Define, for every $n \in \mathbb{N}$,

$$P_k(n) := \frac{\#\{\mathbf{i} \in \cup_{0 \leq i \leq n} \mathbb{G}_i : Z_{\mathbf{i}} = k\}}{2^{n+1}} \quad (k \in \mathbb{N}).$$

Theorem 3. *If $\mathbb{E}(\log(f'(1))) < 0$ and $\max(\mathbb{E}(\log^+(Y_i)) : i = 0, 1) < \infty$, then $(P_k(n))_{k \in \mathbb{N}}$ converges in probability in $\mathbb{S}^1(\mathbb{N})$ to the deterministic sequence $(f_k)_{k \in \mathbb{N}}$ as $n \rightarrow \infty$. Moreover for every $k \in \mathbb{N}$, $\sqrt{n}(P_k(n) - f_k)$ converges in distribution to a centered normal law as $n \rightarrow \infty$, with a non explicit variance.*

Proof. Use again Theorem 1 (i) and Theorem 8 in [12] to prove the law of large numbers. For the central limit theorem, use Theorem 19 in [12] by letting F be the set of continuous functions taking values in $[0, 1]$. \square

6.3 Asymptotics with contamination in the case $\mathbb{E}(\log(f'(1))) \geq 0$ or $\max(\mathbb{E}(\log^+(Y_i)) : i = 0, 1) = \infty$.

In this case, cells become infinitely infected as the generation tends to infinity.

Theorem 4. *If $\mathbb{E}(\log(f'(1))) \geq 0$ or $\max(\mathbb{E}(\log^+(Y_i)) : i = 0, 1) = \infty$, for every $k \in \mathbb{N}$, then $F_k(n)$ tends to zero as $n \rightarrow \infty$. That is, for every $K \in \mathbb{N}$,*

$$\lim_{n \rightarrow \infty} \#\{\mathbf{i} \in \mathbb{G}_n : Z_{\mathbf{i}} \geq K\}/2^n \stackrel{\mathbb{P}}{=} 1.$$

Proof. By Fubini's theorem, we have

$$\begin{aligned} \mathbb{E}[\#\{\mathbf{i} \in \mathbb{G}_n : Z_{\mathbf{i}} \geq K\}/2^n] &= \sum_{\mathbf{i} \in \mathbb{G}_n} \mathbb{P}(Z_{\mathbf{i}} \geq K)/2^n \\ &= \sum_{\mathbf{i} \in \mathbb{G}_n} \mathbb{P}((a_0, \dots, a_{n-1}) = \mathbf{i}) \mathbb{P}(Z_{\mathbf{i}} \geq K) \\ &= \mathbb{P}(Z_n \geq K). \end{aligned}$$

By Theorem 1, $\mathbb{P}(Z_n \geq K)$ tends to 1, then $1 - \#\{\mathbf{i} \in \mathbb{G}_n : Z_{\mathbf{i}} \geq K\}/2^n$ converges to 0 in L^1 , which gives the result. \square

7 Asymptotics for the number of parasites

We assume here that parasites multiply following a Galton Watson process with deterministic mean m , independently of the cell they belong to. That is, $s \mapsto \mathbf{f}(s, s)$ is deterministic and every parasite multiply independently with the reproduction law whose p.g.f. is equal to $g : s \mapsto \mathbf{f}(s, s)$. Moreover we assume that contamination of a cell does not depend on the number of enclosed parasites. That is

$$Y \stackrel{d}{=} Y_0 \stackrel{d}{=} Y_1.$$

Set P_n the number of parasites in generation n . Without contamination, in the supercritical case $m > 1$, it is well know that either P_n becomes extinct or P_n/m^n converges to a positive finite random variable. In the presence of contamination, we have the following result.

Proposition 3. *If $\mathbb{E}(Y) < \infty$ and $\mathbb{P}(Y_0 > 0) > 0$, then $\log(P_n)/n$ converges in \mathbb{P} to $\log(\max(2, m))$.*

Proof. First, we prove the lower bound. This is a consequence of the fact that P_n is larger than

- (i) the total number of parasites P_n^1 which contaminate cells of generation n ,
- (ii) the number of parasites $P_n(p)$ in generation n with the same given parasite ancestor in generation p .

Indeed, first P_n^1 is the sum of 2^n i.i.d. random variables with mean $\mathbb{E}(Y)$, so law of large numbers ensures that

$$P_n^1/2^n \xrightarrow{n \rightarrow \infty} \mathbb{E}(Y) > 0 \quad \text{in } \mathbb{P}$$

Then, since $P_n \geq P_n^1$ a.s. for every $n \in \mathbb{N}$,

$$P_n \xrightarrow{n \rightarrow \infty} \infty \quad \text{in } \mathbb{P}. \quad (16)$$

Moreover for every $p < n$,

$$P_n(p)/m^{n-p} \xrightarrow{n \rightarrow \infty} W, \quad \text{a.s.}, \quad (17)$$

with $\mathbb{P}(W > 0) > 0$. Let now P_n^2 be the sum of the number of descendants in generation n of each parasite of generation p . We get then the sum of P_p i.i.d. quantities distributed as $P_n(p)$. Then (16) and (17) ensure that we can choose p such that

$$P_n^2/m^{n-p} \xrightarrow{n \rightarrow \infty} W' \quad \text{a.s.}$$

with $\mathbb{P}(W' > 0) \geq 1 - \epsilon$.

Using that N_n is larger than P_n^1 and P_n^2 ensures that for every $\epsilon > 0$,

$$\limsup_{n \rightarrow \infty} \mathbb{P}(\log(P_n)/n \leq \log(\max(2, m))) < \epsilon.$$

Letting $\epsilon \rightarrow 0$ gives the lower bound.

Second, we prove the upper bound. Note that the total number of parasites in generation n can be written as

$$P_n = \sum_{i=1}^n \sum_{j=1}^{2^i} \sum_{k=1}^{Y^{i,j}} Z_k^{i,j},$$

where $Y^{i,j}$ is the number of parasites which contaminate the j th cell of generation i , and labeling by $1 \leq k \leq Y^{i,j}$ these parasites, $Z_k^{i,j}$ is the number of descendants in generation n of the k th parasites.

Moreover $(Y^{i,j} : i \in \mathbb{N}, j \in \mathbb{N})$ are identically distributed and independent of $(Z_p^{i,j}(k), i \in \mathbb{N}, j \in \mathbb{N}, k \in \mathbb{N})$, $(Z_k^{i,j}, i \in \mathbb{N}, j \in \mathbb{N}, k \in \mathbb{N})$ are independent and $Z_p^{i,j}(k)$ is the population of a Galton Watson process in generation $n - i$ with offspring probability generation function equal to g . Thus

$$\begin{aligned} \mathbb{E}(P_n) &= \sum_{i=1}^n \sum_{j=1}^{2^i} \mathbb{E}(\sum_{k=1}^{Y^{i,j}} Z_k^{i,j}) \\ &= \sum_{i=1}^n \sum_{j=1}^{2^i} \mathbb{E}(Y^{i,j}) \mathbb{E}(Z_k^{i,j}) \\ &= \mathbb{E}(Y) \sum_{i=1}^n \sum_{j=1}^{2^i} m^{n-i} \\ &= 2\mathbb{E}(Y) \frac{m^n - 2^n}{m - 2} \quad \text{if } m \neq 2. \end{aligned}$$

If $m = 2$, then $\mathbb{E}(P_n) = \mathbb{E}(Y)nm^n$. This gives the upper bound by Markov inequality and completes the proof. \square

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